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Relationships Among Humus Forms, Forest Floor Nutrient Properties, and Understory Vegetation

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ABSTRACT. Morphologically characterized humus forms and their associated understory vegetation have been used to infer different modes of decomposition of forest floor materials, but few studies have analyzed relationships among humus forms, forest floor nutrient properties, and understory vegetation. Examination of these relationships was accomplished in this study by a numerical analysis of forest floor and vegetation data that were obtained from 151 cool mesothermal forest ecosystems of southern British Columbia and stratified into seven humus form groups. Four forest floor nutrient properties (pH, C/N ratio, total N, and sum of exchangeable Ca, Mg, and K) and nine diagnostic combinations of species differentiated the groups. pH and mineralizable-N consistently increased, and C/N ratio consistently decreased from Lignomors to Hemimors, Humimors, Mormoders, Leptomoders, and to Vermimulls, indicating the presence of a regional decomposition gradient. Multivariate summaries of the nutrient properties and diagnostic species were highly correlated. A consistent correlation was also found between the nutrient properties and indicator plants of nitrogen-rich soils. FOR. SCI. 36(3):564–581.

ADDITIONAL KEY WORDS. Humus form classification, diagnostic species, indicator species, multivariate analysis.

THE HUMUS FORM (MÜLLER 1878) IS DEFINED as a group of soil horizons located at or near the surface of a pedon which have formed from organic residues, either separate from, or intermixed with, mineral materials (Klinka et al. 1981). Thus a humus form may be comprised of entirely organic, or both mineral and organic horizons. The mineral horizons which are included in humus forms are restricted to melanized A horizons characterized by accumulation of organic matter from residues of root systems or the activity of soil fauna, both of which may be associated with infiltration.

Humus forms function as the habitat of decomposer organisms and as a nutrient sink and resource. These functions are reflected in morphological characteristics of humus form horizons that manifest the mode and rate of decomposition, and nutrient availability for higher plants (e.g., Wilde 1958, Kononova 1961, Pritchett 1979, Duchaufour 1982, Carlyle 1986).

Considerable attention has been given to the systematic description and classification of humus forms (e.g., Müller 1878, Romell and Heiberg 1931, Hoover and Lunt 1952, Kubiena 1953, Wilde 1954, 1966, 1971, Bernier 1968, Klinka et al. 1981); however, some of these workers, and others (e.g., Mader 1953, Barratt 1974, Howard 1969, Lowe and Klinka 1981, Lowe et al. 1987) have also

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attempted to characterize morphologically defined humus form taxa by inorganic and organic constituents.

A synopsis of humus form orders, groups, and subgroups pertinent to this paper follows (Table 2); however, more complete information is given in the first approximation of the "Taxonomic Classification of Humus Forms in Ecosystems of British Columbia" (Klinka et al. 1981). This classification segregates Mors from Moders and Mulls by the presence of the **F** horizon that has a matted fabric usually interwoven by fungal mycelia (the **Fq** diagnostic horizon) (Wilde 1966, Bernier 1968, Babel 1975). The **F** ("fermented") horizon corresponds partly to the O1 and O2 horizons of the Soil Survey Staff (1975).

Four groups of the Mor order are pertinent to this study: Totilignomors, Hemimors, Hemihumimors, and Humimors. The dark gray **H** (humus) horizon [similar to the O2 horizon of the Soil Survey Staff (1975)] in which fine organic substances predominate over plant residues (the diagnostic **Hd** horizon) constitutes <35% of the combined thickness of the **F** and **H** horizons in Hemimors, ⩾35 but <70% Hemihumimors, and ⩾70% in Humimors. Lignic subgroups of Mors have ⩾35 but <70% (by volume) of the humus form profile made of decaying coniferous wood. Totolignomor (a tentative humus form group) represents the extreme case where these lignic subgroups of Mors are comprised largely of decaying coniferous wood (⩾70% by volume). Residuic subgroups of Mors have **H** horizons that contain fine, dark reddish brown root or ligneous residues which are resistant to decomposition (the **Hr** diagnostic horizons).

Two groups of the Moder order are examined: Mormoders and Leptomoders. Mormoders have **F** horizons that are weakly matted by fungal mycelia and contain a considerable amount of insect and arthropods droppings (the **Fqa** diagnostic horizon). Leptomoders have friable and granular **F** and **H** horizons with abundant droppings of soil fauna (the diagnostic **Fa** and **Ha** horizons) (Wilde 1966, Bernier 1968, Babel 1975).

Vermimulls are the only group of the Mull order discussed in this study. Vermimulls have thin **Fa** horizons, absent or incipient **Ha** horizons, and diagnostic melanized A horizons ⩾2 cm thick.

Due to its role in nutrient storage and cycling, and in influencing temperature and moisture regimes of soils, humus form has been considered an essential component of ecological site quality (Sukachev and Dylis 1964). In British Columbia, three humus form orders—Mor, Moder, and Mull—have been used as one of the major determinants in field identification of nutrient regimes of forest soils (Klinka *et al.* 1984). The identification of humus forms may be facilitated by understory vegetation providing that systematic affinities between humus forms and understory vegetation exist on a regional basis. Understory species that have roots almost completely confined to the humus form should exhibit a well-defined spatial pattern reflecting the humus form. Regardless of differences in regional climate and flora, distinct spatial patterning of vegetation at the humus form level is known to occur (e.g., Ellenberg 1974, Anonymous 1978, Klinka et al. 1989).

The present study examines relationships of humus form taxa defined by Klinka et al. (1981) to (1) selected humus form nutrient properties and (2) associated understory vegetation, without intending to resolve cause and effect relationships between humus form and vegetation. The objective was to determine to what extent forest floor nutrient properties or understory vegetation segregate some common humus form taxa, and to evaluate the usefulness of understory vegetation as an indicator of humus form quality.

MATERIALS AND METHODS

This study used the humus form and vegetation data of studies carried out in the University of British Columbia Research Forest (Klinka 1976) and on Vancouver Island (Kabzems 1985, Klinka, pers. comm., Nuszdorfer, pers. comm.). All these studies employed the same sampling and analytical methods for both humus forms and vegetation of unmanaged, late-seral ecosystems located within the submontane maritime subzones of the Coastal Western Hemlock zone (Krajina 1969). A total of 151 sites (ecosystems) were used for the analysis representing a geographically and taxonomically wide range of terrestrial humus forms and vegetation. The analysis of forest floor nutrient properties also included seven samples of decayed coniferous wood.

At each site, a sample plot (0.04 ha in size) was chosen to represent a segment of landscape relatively uniform in climate, soil, and plants. Description of vegetation and site characteristics followed the methods outlined in Pojar et al. (1987). Vegetation description included identification of all vascular plants, bryophytes, and lichens and estimates of cover for each species using the Domin-Krajina species significance scale (Mueller-Dombois and Ellenberg 1974). Species growing as epiphytes and on decaying wood or coarse fragments and rock were not included in the analysis.

A soil pit was excavated approximately 1 m^2 in plan area and to the base of the control section (Soil Survey Staff 1975) in each site. The area adjacent to this soil pit was used to describe and sample the humus form of the site. Humus form subgroups were identified according to the taxonomic classification of Klinka et al. (1981) using the presence, sequence, and relative thickness of diagnostic horizons. Each humus form sample was a composite of all of its organic horizons. Mulls and other taxa with melanized A horizons were examined on the basis of the forest floor portion of their humus form profile as these mineral horizons are considered to represent a different population from organic horizons (Lowe and Klinka 1981). In the laboratory, all samples were air-dried to constant mass and ground to 20 mesh size in a Wiley mill. Samples were analyzed for pH in a 1:10 material:water (by mass) slurry using a combination electrode, total C with a Leco induction furnace (Bremner and Tabatabai 1971), total N using a semimicro-Kjeldahl digestion and a Technicon Autoanalyzer (Anonymous 1976), and exchangeable cations (Ca, Mg, and K) using 1 M ammonium acetate adjusted to pH 7 and atomic absorption spectrophotometry (Heald 1965). Mineralizable-N was determined using the anaerobic incubation method of Powers (1980) with released NH_4 determined colorimetrically using a Technicon Autoanalyzer.

Diagnostic combinations of species present in the understory were used to differentiate humus form taxa, excluding Totilignomors which were not floristically described. These diagnostic combinations were identified using the Braun-Blanquet tabular method (Westhoff and van der Maarel 1980), VTAB tabling program (Emanuel 1987), and species with differential or dominant-differential diagnostic values (Pojar et al. 1987). The diagnostic values of species were defined as follows: differential species—present in one or more taxa under comparison, presence class $\geqslant$III (frequency $>$41%) and at least two presence classes greater than in other taxa of the same categorical rank and circumscription; dominant-differential species—present and dominant in one or more taxa under comparison, presence class $\geqslant$III (frequency $>$41%), mean species significance

$\geqslant 5$ (cover $\geqslant 10\%$) and two or more significance classes greater than in other taxa of the same categorical rank and circumscription.

Complementary to diagnostic combinations of species, computer-assisted spectral analysis (Mueller-Dombois and Ellenberg 1974, Emanuel 1987) was carried out to determine relative frequencies of nitrogen indicator species groups (NISGs) which have been related to low, intermediate, and high levels of available soil nitrogen (Klinka et al. 1989). The relative frequency was calculated for each site as follows (Green et al. 1989):

$$F_{NISG_j} = (SUM_i C_{ij} / SUM_{ij} C_{ij}) \times 100$$

where C_{ij} is the midpoint percent cover for indicator species i in $NISG_j$.

Humus form properties were tested for homogeneity of variance using Bartlett's procedure (Zar 1984). Cluster analysis (Fox and Guire 1976), one-way ANOVA (Grieg and Osterlin 1978), and multiple comparisons of group means using Scheffe's test (Zar 1984) were conducted to detect differences between humus form taxa and humus form nutrient properties. Regression analysis was employed to examine relationships between nitrophytic species, nutrient properties, and the nutrient properties summarized by the first two PCA axes (Chatterjee and Price 1977).

Due to a large vegetation data base, the original matrix (151, 290) was progressively reduced until it contained only diagnostic species (see Table 7). The effect of removing species from the data set was examined using progressively smaller matrices—(151, 143), (151, 112) and (151, 35)—and Q-type principal components analyses (PCAs) (Pimental 1979). Comparison of the results of all PCAs suggests that the matrix using 35 diagnostic species (151, 35) produces nearly the same results as the original matrix (Table 1).

Multivariate relationships were examined by PCA performed on a correlation matrix (Noy-Meir and Whittaker 1977). Overall eigenstructure and significance of axes extracted by PCA were evaluated by tests of variable independence and equicorrelation (Morrison 1976). Extracted component scores were submitted to one-way MANOVA, and the likelihood ratio criterion (Rao 1973) was used to determine whether the vector of means was the same for the first two component

TABLE 1.

Results of the PCA on understory vegetation using the original and reduced data matrices.

Number of species	290	143	112	35
Variance explained by first 10 PCA axes	63.2	67.3	68.7	81.1
First two eigenvalues	51.9	49.5	49.3	44.1
	21.8	21.2	21.0	15.6
Five species[1] most highly correlated to the first component				
Athyrium filix-femina	0.706	0.727	0.728	0.745
Gaultheria shallon	−0.789	−0.789	−0.789	−0.816
Plagiomnium insigne	0.715	0.713	0.713	0.741
Polystichum munitum	0.833	0.835	0.835	0.845
Rubus spectabilis	0.665	0.689	0.691	0.720

[1] Selected from the data matrix including 35 species.

scores across the range of humus form taxa. Relationships between the principal components and humus form or vegetation variables were examined by correlating component scores with values for individual variables ("component correlation," Pimentel 1979). To avoid cluttering the PCA ordination with a large number of plots, humus form taxa were represented by 95% confidence ellipses (Owen and Chmielewski 1985), which were based on the first two component scores of humus form or vegetation data.

Stepwise discriminant analysis (forward selection) (Seal 1964, Dixon 1977) was carried out to test the ability of humus form nutrient properties in differentiating humus form taxa. The success of differentiation was assessed on a jack-knifed classification matrix (Dixon 1977).

Relationships between humus forms and understory vegetation were explored using canonical correlation analysis (CCA) (Anonymous 1982). Both nutrient and vegetation variables were summarized with PCA. CCA was then performed using the first PCA axis of the humus form data and the first PCA axis of the vegetation data. Each CCA was followed by component correlation between canonical variates and the original variables submitted to PCA. Correlations among nutrient properties, diagnostic species, PCA axes, and canonical variates were used to interpret the results of the CCA (Gittins 1985).

RESULTS

RELATIONSHIPS BETWEEN HUMUS FORMS AND HUMUS FORM NUTRIENT PROPERTIES

The correlation between pH and C/N was strongly negative ($r = -0.68$; $r_{0.01} = 0.21$), suggesting an increase in microbial activity with increasing pH. Groupings identified on the basis of a cluster analysis of pH, C/N, total N (tN), and sum of exchangeable Ca, Mg, and K (SEC) showed a poor taxonomic relationship within the Mor order (Table 2). Therefore, both humus form and vegetation data were restratified according to a revised classification based on the obtained clusters with further analysis limited to seven humus form taxa (Table 2). Firstly, this revised classification resulted in deletion of the Hemihumimor group. Hemihumimors with <50% of the combined thickness of F and H horizons were assigned to Hemimors and those with ≥50% to Humimors. Secondly, Totilignomors, Lignohemimors, Lignohumimors, Residuohemimors, Residuohumimors were placed in a new group—Lignomors, with three new subgroups—Orthilignomors, Resilignomors, and Totilignomors. The formative element "Resi" replaced "Residuo," for brevity. Thirdly, the Mormoder group and its subgroups were placed in the Mor order.

There was a general trend of increasing pH and decreasing C/N from Totilignomors to Lignomors, Hemimors, Humimors, Mormoders, Leptomoders, and to Vermimulls. Total N and SEC did not appear to form a distinct gradient. With the exception of Totilignomors, the other groups did not represent discrete entities in any single attribute. Mineralizable N (minN) did show a distinct gradient and range ($P \leq 0.05$) across each of the five groups for which data were available (Table 3). Due to a small number of samples and large variation in the C/N ratio, Totilignomors were excluded from further analyses.

TABLE 2.

Synopsis of humus form orders, groups, and subgroups of this study showing the original (left column) and revised (right column) classification. Supercripts in the left column mark groupings obtained in cluster analysis, in the right column the humus form taxa used in further analysis.

Order	Group	Subgroup	Order	Group	Subgroup
Mor			**Mor**		
	Totilignomor^{1}			Lignomor^{2}	
	Hemimor				Orthilignomor^{2}
		Orthihemimor^{3}			Resilignomor^{2}
		Lignohemimor^{2}			Totilignomor
	Hemihumimor			Hemimor^{3}	
		Orthihemihumimor^{3,4}			Orthihemimor
		Lignohemihumimor^{2}		Humimor^{4}	
		Residuohemihumimor^{2}			Orthihumimor
	Humimor			Mormoder^{5}	
		Orthihumimor^{4}			Orthimormoder
		Lignohumimor^{2}			Humimormoder
		Residuohumimor^{2}			
Moder			**Moder**		
	Mormoder			Leptomoder^{6}	
		Orthimormoder^{5}			Orthileptomoder
		Humimormoder^{5}			Hemileptomoder
	Leptomoder				
		Orthileptomoder^{6}			
		Hemileptomoder^{6}			
Mull			**Mull**		
	Vermimull			Vermimull^{7}	
		Orthivermimull^{7}			Orthivermimull

The first two axes of the PCA ordination based on pH, C/N, TN, and SEC expressed nearly 100% of the total variance. The first axis, which accounted for 67% of the variance, suggested that there was a major trend of increasing C/N and SEC with decreasing pH (Table 4). The inverse relationship between SEC and pH is contrary to the result of simple correlations and seems to reflect two anomalies in the data set: the high SEC and low pH values of Lignomors and the low SEC and high pH values of Vermimulls (Table 3). These anomalies likely reflect relatively lower cation exchange capacities (CECs) in L horizons than in F and H horizons. Consequently, Lignomors, with their thicker F and H horizons may have high SECs and a relatively lower base saturation (BS) while Vermimulls may have lower SECs and a relatively higher BS.

Confidence ellipses calculated from the PCA ordination of 151 sample plots show the humus form groups occur along the first axis (from left to right) in a similar but reversed sequence to that shown in Table 3 (Figure 1). Multiple comparisons using linear contrasts and Bonferroni critical levels (Miller 1985) following MANOVA on the first two component scores found all groups except Hemimors, Humimors, and Mormoders to be distinct ($P \leqslant 0.05$). The nearly

TABLE 3.

Means and standard deviations (in parentheses) of humus form pH (H_2O), carbon:nitrogen ratio (C/N), total nitrogen (tN), sum of exchangeable cations (SEC)—Ca, Mg, and K and mineralizable-N (minN) in seven humus form taxa. The same superscript indicates homogeneous subsets at $P \leqslant .05$ (Scheffe's test).

Humus form group	n	pH	C/N	tN gKg^{-1}	SEC $cmol_ckg^{-1}$	minN[1,2] 10^3gKg^{-1}
Totilignomors[1]	7	3.5^{A}	172^{A}	5.2^{A}	14.0^{A}	38^{A}
		(0.4)	(174)	(.34)	(4.96)	(15)
Lignomors[2,3]	34	3.8^{B}	54^{B}	9.5^{B}	27.7^{B}	196^{B}
		(0.3)	(9.4)	(.14)	(9.41)	(36)
Hemimors[4]	14	$3.7^{A,B}$	$36^{B,C}$	14.0^{D}	15.4^{A}	
		(0.2)	(4.7)	(.22)	(4.30)	
Humimors[4]	16	3.9^{B}	$35^{B,C}$	14.3^{D}	16.4^{A}	
		(0.2)	(4.4)	(.23)	(4.41)	
Mormoders[2,4,5]	24	3.8^{B}	$36^{B,C}$	12.2^{C}	23.5^{B}	360^{C}
		(0.4)	(5.5)	(.20)	(11.3)	(91)
Leptomoders[2,4]	36	$4.3^{D,C}$	27^{C}	14.2^{D}	24.4^{B}	519^{D}
		(0.4)	(8.4)	(.36)	(16.2)	(120)
Vermimulls[2,4]	27	5.1^{D}	17^{C}	7.0^{A}	11.4^{A}	779^{E}
		(0.4)	(5.3)	(.39)	(12.0)	(147)

[1] Klinka (pers. comm.): data from northern Vancouver Island.

[2] Kabzems (1985): data from Cowichan Lake area on Vanouver Island; mean minN values are based on 4 plots for Lignomors, 8 plots for Mormoders, 8 plots for Leptomoders, and 4 plots for Vermimulls, with 3 composites of 5 subsamples per plot.

[3] Nuszdorfer (per. comm.): data from northern Vancouver Island.

[4] Klinka (1976): data from the University of British Columbia Research Forest on coastal mainland.

[5] Klinka (pers. comm.): data from highly productive western hemlock sites on Vancouver Island.

complete overlap of confidence ellipses for these three groups illustrates their similarities in pH, C/N, tN, and SEC characteristics (Table 3).

Discriminant analysis based on pH, C/N, tN, and SEC correctly classified 71.5% of the plots into their source groups (Table 5). C/N had the greatest contribution to the classification, and Hemimors and Humimors were found to represent a single group ($P \leqslant .05$). "Misclassifications" of individual samples suggested by the analysis were mostly confined to adjacent humus form groups.

The poor differentiation of Hemimors and Humimors was due to similarities in

TABLE 4.

Correlations of forest floor nutrient properties with the first two PCA axes ($r_{0.01} = 0.21$).

Property	Axis 1 66.7%[1]	Axis 2 33.2%[1]
pH	**−0.48**	**0.54**
C/N	**0.89**	**−0.45**
TN	−0.05	**0.22**
SEC	**0.71**	**0.70**

[1] Percent variance explained by the axis.

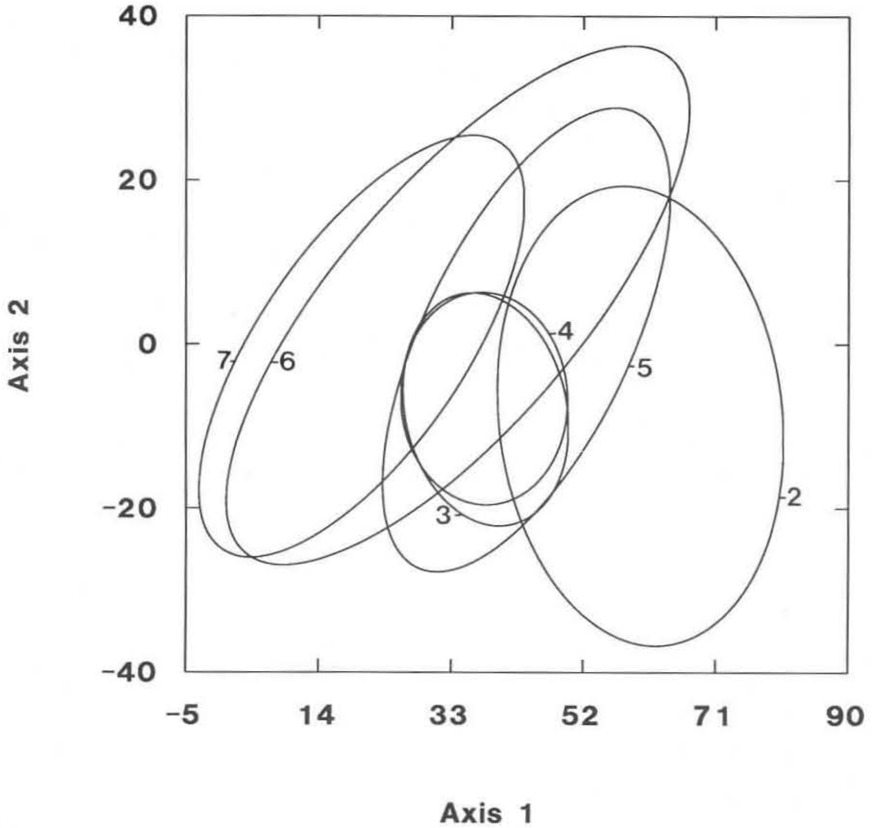

FIGURE 1. Ordination of plots along the first two axis of PCA on humus form nutrient properties showing 95% confidence ellipses for Lignomors (2), Hemimors (3), Humimors (4), Mormoders (5), Leptomoders (6), and Vermimulls (7).

the selected nutrient properties. The weak separation of Mormoders and Leptomoders likely occurred as a result of difficulties in applying the present diagnostic criteria for Fqa horizons (partly fragmented or comminuted by soil fauna) (Lowe and Klinka 1981, Klinka et al. 1981). Combining Hemimors and Humimors greatly improved the classification of the Hemimor/Humimor and Mormoder groups; 90 and 75% of plots, respectively, were correctly identified, while the identification of the remaining groups was unaffected.

RELATIONSHIPS BETWEEN HUMUS FORMS AND UNDERSTORY VEGETATION

Variation in understory vegetation among six humus form groups was summarized through the use of nine (**A** to **I**) diagnostic combinations of species (Table 6). Affinities between understory vegetation and the humus form groups included in a given diagnostic combination of species increase with the number, presence class, and significance class of species within the diagnostic combination of species. Floristic differences between groups also increase with the number, presence class, and significance class of species within a diagnostic combination of species.

TABLE 5.

Percentage of plots identified by discriminant analysis in the source humus form groups on the basis of forest floor nutrient properties. The numerical codes are: 2—Lignomors, 3—Hemimors, 4—Humimors, 5—Mormoders, 6—Leptomoders, 7—Vermimulls.

Humus form group	Percent correct	Number of plots identified in humus form groups					
		2	3	4	5	6	7
2	85.3	**29**	0	0	5	0	0
3	64.3	0	**9**	5	0	0	0
4	50.0	0	6	**8**	1	1	0
5	54.2	1	7	1	**13**	2	0
6	66.7	0	1	4	5	**24**	2
7	92.6	0	0	0	0	2	**25**
Total	71.5	30	23	18	24	29	27

Tabular comparison demonstrated that plant species were not randomly distributed along a regional humus form gradient despite obvious disparities between the size of area used for the humus form sample relative to that used for sampling understory vegetation. The most orderly arrangement of both humus form groups (columns) and diagnostic species (rows) from left to right was according to the sequence from Lignomors to Hemimors, Humimors, Mormoders, Leptomoders, and to Vermimulls. Each group was differentiated by two or three diagnostic combinations of species; for example, the combinations **A** and **F** segregated Mormoders from all other groups (Table 6). Perfect separation, in which each humus form group would be differentiated by the combination unique to this group, was not present in the data set. Two well-expressed diagnostic combinations of species were identified—the **B** combination diagnostic for Lignomors, Hemimors, and Humimors, and the **G** combination diagnostic for Leptomoders and Vermimulls. Other combinations included a few species with an intermediate presence and low cover values.

The 35 diagnostic species were analyzed using PCA. The first two axes accounted for 47% of the total variance and 34 species were significantly correlated with the first, second, or both PCA axes. The species correlated with the first two axes ($P \leq 0.01$) were sorted into four strata according to the sign of correlation: *Dicranum scoparium* (−, −), *Cornus unalaschkensis* (−, +), *Achlys triphylla* (+, −), and *Acer circinatum* (+, +) (Table 7). Values of these species as indicators of available soil nitrogen (Klinka et al. 1989) were included to facilitate interpretation of humus form-understory vegetation relationships.

Species of the *Dicranum scoparium*- and *Cornus unalaschkensis*-strata were correlated negatively with the first axis. These species were associated predominantly with Lignomors, Hemimors, and Humimors (Table 7) (or with the **A, B, C,** or **D** diagnostic combinations of species; Table 6) and were indicators of nitrogen-poor soils. Species of the *Cornus unalaschkensis*-stratum were correlated positively with the second PCA axis and are known to increase with increasing humidity and decreasing temperature of regional climate (Orloci 1964). Species of the *Achlys triphylla*- and *Acer circinatum*-strata were correlated positively with the first axis and scattered in the right region of the ordination. These

TABLE 6.

Diagnostic combinations of species identified for humus form orders and groups.

Code number		2		3		4		5		6		7	
Number of plots		34		14		16		24		36		27	
Humus form taxon and species	Diagnostic value[1]	Presence class[2] and mean species significance[3]											
Mors (2,3,4 & 5)		A											
Gaultheria shallon	(d,cd)	V	8	V	6	V	4	III	5	IV	2	III	1
Hylocomium splendens	(d,cd)	V	6	V	5	V	4	IV	5	IV	3	III	2
Linnaea borealis	(d)	II	2	III	1	III	1	I	2	I	1	I	+
Plagiothecium undulatum	(d,c)	V	3	V	3	V	3	IV	3	III	2	I	1
Rhytidiadelphus loreus	(d,cd)	V	6	V	4	V	4	IV	4	III	2	III	2
Lignomors, Hemimors & Humimors (2,3 & 4)		B											
Cornus unalaschkensis	(d)	III	4	III	1	II	1			II	+	I	+
Gaultheria shallon	(d,cd)	V	8	V	6	V	4	III	5	IV	2	III	1
Linnaea borealis	(d)	II	2	III	1	III	1	I	2	I	1	I	+
Menziesia ferruginea	(d)	III	3	III	1	IV	2	I	+	III	1	II	1
Thuja plicata	(d,c)	V	4	V	4	V	4	II	3	V	4	V	4
Vaccinium alaskaense	(d)	III	3	III	3	IV	3	I	2	II	1	II	+
Lignomors (2)		C											
Gaultheria shallon	(dd)	V	8	V	6	V	4	III	5	IV	2	III	1
Listera cordata	(d)	IV	2	I	+	I	+	I	+				
Vaccinium parvifolium	(dd)	V	5	V	3	V	3	V	5	V	2	V	2
Hemimors (3)				D									
Dicranum scoparium	(d)	I	+	IV	2	I	+	I	+	I	+		
Pleurozium schreberi	(d)	I	+	III	2	I	+						
Pseudotsuga menziesii	(d)	I	2	III	1	I	+	I	1	I	+	I	+
Humimors (4)						E							
Dryopteris expansa	(d)	I	+	II	1	IV	2	II	2	IV	2	V	3
Polystichum munitum	(d,c)	II	1	III	2	V	2	V	4	V	6	V	6
Mormoders (5)								F					
Achlys triphylla	(d)	I	+			I	+	III	4	II	2	II	3
Kindbergia oregana	(d,cd)	III	4	III	5	IV	5	V	6	V	4	IV	3
Mahonia nervosa	(d)	I	+					III	4	II	2		
Polystichum munitum	(d,c)	II	1	III	2	V	2	V	4	V	6	V	6
Moders & Mulls (6 & 7)										G			
Acer circinatum	(d,cd)	I	+	II	1	III	3	I	1	V	5	V	5
Dryopteris expansa	(d,c)	I	+	II	1	IV	2	II	2	IV	2	V	3
Luzula parviflora	(d)	I	+			I	+	I	1	III	+	III	1
Mycelis muralis	(d)							I	+	II	1	III	1
Oplopanax horridus	(d)					I	+	I	+	II	+	III	2
Polystichum munitum	(dd,cd)	II	1	III	2	V	2	V	4	V	6	V	6
Rhizomnium glabrescens	(d)	II	1	II	1	III	2	II	2	IV	3	IV	3
Rubus spectabilis	(d,c)	I	+	II	+	II	1	I	1	IV	3	V	5
Trillium ovatum	(d)			II	+	II	+	I	+	IV	1	III	1
Leptomoders (6)										H			
Plagiothecium undulatum	(d)	V	3	V	3	V	3	IV	3	III	2	I	1
Pteridium aquilinum	(d)	I	+	IV	2	III	1	II	1	IV	1	II	1
Rubus ursinus	(d)	I	+	II	+	III	1	II	1	IV	1	II	+
Vermimulls (7)												I	
Athyrium filix-femina	(d,c)	I	+	II	+	I	+	I	+	III	2	V	3
Galium triflorum	(d,c)							I	1	III	1	V	2
Kindbergia praelonga	(d,c)	I	+							III	1	V	3
Leucolepis menziesii	(d,c)					I	+	I	+	III	2	V	3
Plagiomnium insigne	(d,c)					I	+			III	2	V	4
Rhamnus purshianus	(d)	I	+	I	+	II	+	I	+	I	+	III	1
Rubus spectabilis	(dd,cd)	I	+	II	+	II	1	I	1	IV	3	V	5
Tiarella trifoliata	(d,c)	I	+	II	+	II	1	II	1	III	1	V	4

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[1] Species diagnostic value: d - differential, dd - dominant differential, cd - constant dominant, c - constant (Pojar et al. 1987).

[2] Presence classes as percent of frequency: I = 1-20, II = 21-40, III = 41-60, IV = 61-80, V = 81 -100.

[3] Species significance classes as midpoint percent cover and range: + = 0.2 (0.1 - 0.3), 1 = 0.7 (0.4 - 1.0), 2 = 1.6 (1.1 - 2.1), 3 = 3.6 (2.2 - 5.0), 4 = 7.5 (5.1 - 10.0), 5 = 15.0 (10.1 - 20.0), 6 = 26.5 (20.1 - 33.0), 7 = 41.5 (33.1 - 50.0), 8 = 60.0 (50.1 - 70.0), 9= 85.0 (70.1 - 100).

TABLE 7.

Correlation values ($r_{0.01} = 0.21$) of diagnostic species with the first two PCA axes.

Species	Axis 1 34.6%[2]	Axis 2 12.2%[2]	Indicator value[1]
Dicranum scoparium	**−.24**	**−.85**	N-poor
Kindbergia oregana	−.03	**−.62**	N-medium
Pseudotsuga menziesii	−.12	**−.21**	
Cornus unalaschkensis	**−.52**	**.38**	N-poor
Gaultheria shallon	**−.82**	.09	N-poor
Hylocomium splendens	**−.69**	.15	N-poor
Linnaea borealis	**−.36**	.02	
Listera cordata	**−.62**	.20	N-poor
Menziesia ferruginea	**−.30**	**.43**	N-poor
Plagiothecium undulatum	**−.53**	.20	N-poor
Rhytidiadelphus loreus	**−.66**	**.35**	N-poor
Thuja plicata	−.08	**.24**	
Vaccinium alaskaense	**−.39**	**.35**	N-poor
Vaccinium parvifolium	**−.58**	.01	N-poor
Achlys triphylla	**.25**	**−.69**	N-rich
Galium triflorum	**.61**	**−.23**	N-rich
Mahonia nervosa	.01	**−.68**	N-medium
Mycelis muralis	**.47**	**−.39**	N-rich
Polystichum munitum	**.84**	−.16	N-rich
Pteridium aquilinum	.15	**−.28**	
Rubus ursinus	**.31**	**−.45**	N-medium
Trillium ovatum	**.52**	−.17	N-rich
Acer circinatum	**.68**	**.39**	N-rich
Athyrium filix-femina	**.74**	**.39**	N-rich
Dryopteris expansa	**.60**	**.32**	N-medium
Leucolepis menziesii	**.71**	**.24**	N-rich
Luzula parviflora	**.47**	**.28**	N-medium
Kinbergia praelonga	**.63**	**.44**	N-rich
Oplopanax horridus	**.50**	**.40**	N-rich
Plagiomnium insigne	**.72**	**.25**	N-rich
Rhamnus purshianus	**.28**	**.21**	N-rich
Rhizomnium glabrescens	**.45**	**.35**	N-medium
Rubus spectabilis	**.72**	**.40**	N-rich
Tiarella trifoliata	**.60**	**.21**	N-rich

[1] Indicator value shows membership of a species in one of the three indicator species groups of available nitrogen (Klinka et al. 1989).

[2] Percent variance explained by the axis.

species were associated predominantly with Leptomoders and Vermimulls (or with the **G, H,** and **I** diagnostic combinations of species) and were indicators of nitrogen-rich soils. Species of the *Achlys triphylla*-stratum were correlated negatively with the second PCA axis and are known to decrease with increasing humidity and decreasing temperature of regional climate (Orloci 1964).

The PCA ordination of understory vegetation was further examined in relation to the six humus form groups. Multiple comparisons following MANOVA on the first two component scores found Hemimors were not significantly different from either Lignomors or Humimors; the remaining comparisons were significant at $P \leq 0.05$.

Based on the nutrient properties of each humus form (Table 3) and the joint distribution of species and humus forms (Table 6), the first PCA axis is suggested to represent a decomposition or nutrient gradient, while the second axis appears to reflect variation in regional climate and soil moisture. Species of the *Dicranum scoparium-* and *Cornus unalaschkensis*-strata decrease and those of the *Achlys triphylla-* and *Acer circinatum*-strata increase with decreasing forest floor C/N and increasing pH and minN along the sequence from Lignomors to Vermimulls.

Relationships between component scores of the first PCA axis and a possible nutrient gradient can also be documented by examining relationships between these scores and the relative frequency of the indicator species group of nitrogen-rich soils F_{NISG3}. A simple linear regression model [Equation (1)] showed a strong relationship suggesting that the first axis does reflect a decomposition or nutrient gradient.

$$F_{NISG3} = 42.38 + 5.26(\text{PCA1}) \qquad (1)$$

$$\text{Adjusted } R^2 = 0.73 \quad F = 399 \quad SE = 26.0\% \quad n = 151$$

where PCA1 are component scores of the first PCA axis based on 35 diagnostic species.

Canonical correlation analysis (CCA) extracted two pairs of humus form-vegetation canonical variates. The first pair was highly correlated ($Rc = 0.90$), indicating the presence of strong linear relationships between variation in forest floor nutrient properties and understory vegetation. The second pair was not as highly correlated ($Rc = 0.73$). Humus form groups identified on the basis of these canonical variates are presented as Gaussian bivariate ellipsoids using a 95% confidence region (Wilkinson 1988). With the exception of a few outliers, the ordination of 151 sample plots on the first pair of canonical variates displayed synchrony between the two data sets, with the Vermimulls occurring toward the negative poles and the Lignomors toward the positive poles suggesting a gradient without obvious discontinuities among the humus form groups (Figure 2).

The nutrient properties most highly correlated to the first pair of vegetation and humus form canonical variates were pH (-0.82 and -0.89) and C/N (0.82 and 0.91). Among 26 diagnostic species highly correlated with the first pair of canonical variates, the positively correlated species (of the *Dicranum scoparium-* and *Cornus unalaschkensis-* strata) were associated with Lignomors, Hemimors, and Humimors and the negatively correlated species (of the *Achlys triphylla-* and *Acer circinatum*-strata) were associated with Leptomoders and Vermimulls. These correlations indicate that the former species (indicators of nitrogen-poor soils) decrease and the latter species (indicators of nitrogen-rich soils) increase with increasing pH and decreasing C/N of the humus form.

In view of strong relationships between humus forms and indicator plants, the possibility of summarizing humus form nutrient properties through the use of indicator species of nitrogen-rich soils was explored. The intent was to evaluate possible relationships, not to give quantitative predictions of the nutrient properties.

The F_{NISG3} increased exponentially in order from 1.31% in Lignomors to 85.0% in Vermimulls (Table 8). ANOVA and multiple comparison of group means showed that three pairs—the Lignomors and Hemimors; Hemimors and Humimors; and Humimors and Mormoders—appeared to have similar frequencies ($P \leqslant .05$).

To quantify relationships between the F_{NISG3} and forest floor nutrient variables

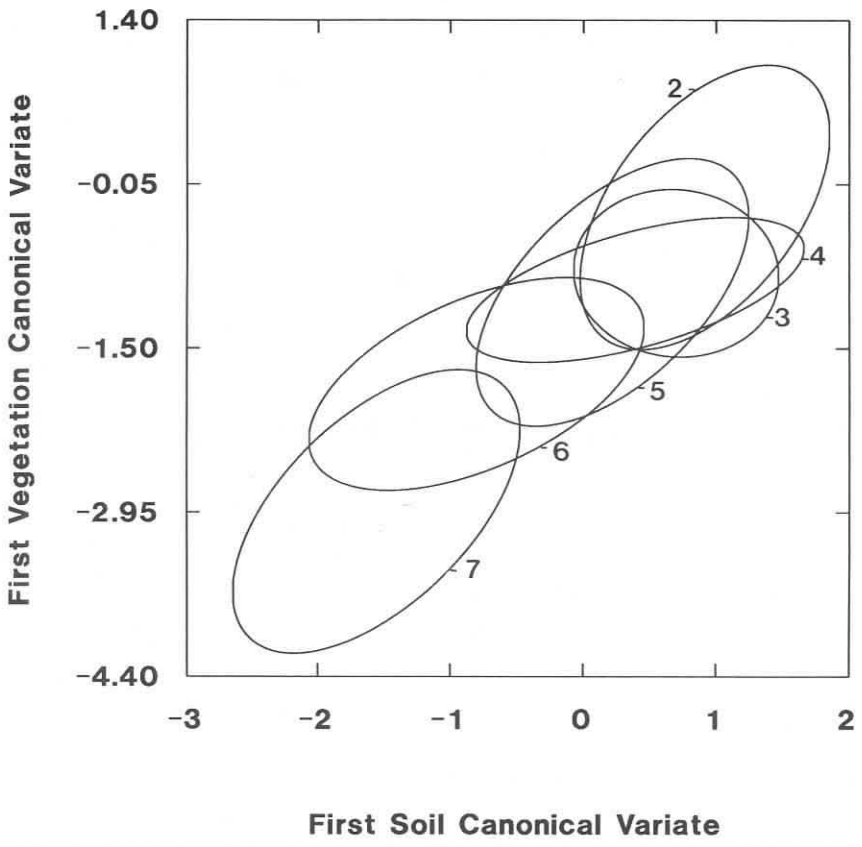

FIGURE 2. Relationships between forest floor nutrient properties and diagnostic species in six humus form groups using the first canonical variates. The numerical symbols for ellipsoids are: Lignomors (2), Hemimors (3), Humimors (4), Mormoders (5), Leptomoders (6), and Vermimulls (7).

two linear regression models [Equations (2) and (3)] and one nonlinear regression model using a natural logarithm transformation [Equation (4)] were developed. All models were significant at ($P \leqslant 0.01$):

$$F_{NISG3} = 98.9 - 1.48(\mathrm{PCA1}) + 1.42(\mathrm{PCA2}) \tag{2}$$

$$\text{Adjusted } R^2 = 0.474 \quad F = 68.5 \quad SE = 29.7\% \quad n = 151$$

TABLE 8.

Means and standard deviations (s.d.) of relative frequencies of indicators species of nitrogen-rich soils (F_{NISG3}). The numerical codes are: 2—Lignomors, 3—Hemimors, 4—Humimors, 5—Mormoders, 6—Leptomoders, 7—Vermimulls. The same superscript indicate homogeneous subsets at $P \leqslant 0.05$.

	2	3	4	5	6	7
Mean	1.31^{A}	$3.24^{A,B}$	$13.9^{B,C}$	23.8^{C}	66.7^{D}	85.0^{E}
s.d.	0.27	8.60	20.9	25.5	35.6	26.6
n	34	14	16	24	36	27

where PCA1 and PCA2 are component scores of the first two axes of the PCA based on forest floor nutrient properties.

$$F_{NISG3} = -3.83 + 23.5(\mathrm{pH}) + 1.36(\mathrm{C/N}) - 13.9(\mathrm{tN}) + 0.7(\mathrm{SEC}) \quad (3)$$

$$\text{Adjusted } R^2 = 0.572 \quad F = 51.2 \quad SE = 26.7\% \quad n = 151$$

$$F_{NISG3} = (2.7)10^{-9}(\mathrm{min}N^{3.75}) \quad (4)$$

$$\text{Adjusted } R^2 = 0.785 \quad F = 85.0 \quad SE = 25.2\% \quad n = 24$$

These models indicate that indices of nutrient availability based on indicator plant species are supported by variation in forest floor form nutrient properties, particularly min*N*.

DISCUSSION

Uncertainties over the choice of appropriate indices and analytical methods have made characterization of decomposition and nutrient availability of humus forms difficult. Despite attempts to develop indices reflecting overall biological activity and decomposition rates based on organic constituents of humus forms (e.g., Lowe 1974, Lowe and Klinka 1981, Lowe et al. 1987), pH and C/N have been the most convenient indices. This study selected inorganic nutrient properties which are commonly used in routine soil analysis because of their relative speed and simplicity of laboratory procedures, and their demonstrated significance for diagnostic purposes (op. cit., Courtin et al. 1989). Recent studies by Kabzems and Klinka (1987), and Klinka and Carter (1990) support the choice of these properties but identify min*N* as the best single index for characterization of a regional nutrient gradient. As data of this study were incomplete, the usefulness of min*N* could not be conclusively proven.

The taxonomic classification proposed by Klinka et al. (1981) is based entirely on morphological characteristics. Any taxonomic classification that strives to show relationships across the full range of its taxa to properties other than those used as differentiating characteristics will eventually require revision. The revision proposed in this study showed that humus form groups reflect a considerable portion of the variation in forest floor nutrient properties as well as understory vegetation. Lignic and residue Mors appear to be better placed in a hierarchy as subgroups of the Lignomor group, and Mormoders as a group of the Mor order. Combining morphologically contrasting Hemimors and Humimors into a single group on the basis of their similarities in four nutrient properties should probably be avoided. Other studies (Lowe and Klinka 1981, Lowe et al. 1987) suggest that other covarying biological, chemical, or physical properties may support the significance of these groups.

Subgroups were not successfully differentiated within their circumscribing groups. This exemplified within group similarities in decomposition which was the intent of the classification. Subgroups are intended to segregate humus forms of a group on the basis of differences in kind and fabric of materials and horizon sequence, i.e., properties without an influential linkage to decomposition.

Differences in the inferred availability of nutrients and the frequency of indicator plants of nitrogen-rich soils suggest that humus forms can be related to segments of a nutrient gradient and thus have important implications for characterizing nutrient regimes of forest soils. However, humus form alone represents only one of the many components of an ecosystem's nutrient cycle. Therefore, humus forms alone cannot be expected to explain all of the variation in soil nutrient levels or the availability of soil nutrients to plants.

Structures of the humus form and vegetation data sets were strongly related. Relationships were revealed in the structure of nutrient properties, diagnostic species, and indicator species of nitrogen-rich soils. Using C/N ratio as an index of decomposition, a regional gradient of increasing decomposition and nutrient availability became apparent when humus forms groups were arranged in order from Lignomors to Hemimors, Humimors, Mormoders, Leptomoders, and to Vermimulls. These results are consistent with reports from other regions of coniferous vegetation and temperate climate (e.g., Anonymous 1978, Carlyle 1986).

Results of the analysis of humus form-understory vegetation relationships were likely weakened by disparities between the sampling area used for humus forms (<1 m^2) and vegetation (400 m^2). The minimal sampling for humus forms has not yet been defined but will likely coincide or be smaller than that of a pedon (Soil Survey Staff 1975). Roemer (1972) identified the minimal sampling area for forest communities to be within the range from 128 to 256 m^2.

As the products of biologically mediated decomposition processes, humus forms vary considerably among plant communities as well as within a plant community. This study suggests that the floristic variation within a plant community reflects the spatial pattern in humus forms on a site. The vegetation description of any study site might have included humus forms of two or more different groups. Although the area of a plant community usually features a dominant humus form (e.g., Lohmeyer and Zezschwits 1982), it is common in old-growth forests for Mors to develop within Moder- or Mull-dominated sites on special microsites formed by downed coniferous logs or stumps in advanced stages of decay; similarly, it is common for Moders or even Mulls to develop within Mor-dominated sites on upturned root mats of mounds formed by wind-thrown trees. The presence of "nonconforming" humus forms or special microsites is reflected in the low presence or cover of "nonconforming" species on a site. For example, *Gaultheria shallon,* a species characteristic of Mors and an indicator of nitrogen-poor soils, occurred on Moder- or Mull-dominated sites, and *Polystichum munitum,* a species characteristic of Moders and Mulls and an indicator of nitrogen-rich soils, occurred on Mor-dominated sites (see Table 6).

Although diagnostic species could assist in field identification of humus form groups on a regional basis, temporal variation in vegetation ecosystems would continually date any key developed for this purpose. Understory vegetation will likely be most useful for recognizing the distribution of contrasting humus forms through examination of the spatial pattern of indicator species of available soil-nitrogen.

CONCLUSIONS

Testing of humus form taxa in relation to forest floor pH, C/N, tN, minN, and SEC and associated understory vegetation showed a poor relationship to subgroups, and suggested revision of the Mor order. Following the revision, the humus form groups examined were found to be strongly correlated to C/N and indicator species of available soil nitrogen, both reflecting rates of decomposition. It is recommended that future taxonomic revisions demonstrate relationships to one or more of the biological, chemical, physical, and vegetation properties in order to improve our understanding and identification of humus forms and to facilitate their management.

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